

A GENERIC REVISION OF THE BRACKISH-WATER SERPULID
FICOPOMATUS SOUTHERN 1921 (POLYCHAETA: SERPULINAE),
INCLUDING *MERCIERELLA* FAUVEL 1923, *SPHAEROPOMATUS*
TREADWELL 1934, *MERCIERELLOPSIS* RIOJA 1945 AND
NEOPOMATUS PILLAI 1960

H. A. TEN HOVE AND J. C. A. WEERDENBURG

*Laboratory for Zoological Ecology and Taxonomy, State University of Utrecht,
Plompstorengracht 9-11, Utrecht, The Netherlands*

In the last half century, five monotypic serpulid genera have been described exclusively from brackish waters, and Pillai (1960) has united four of them in the subfamily Ficopomatinae (see below). One of these, *Mercierella*, has received the attention of many biologists in various fields of research. There has been considerable confusion about the identity of two of the species, namely, *Mercierella enigmatica* and *Neopomatus uschakovi* (see lists of synonyms in this paper). This confusion, and the view of the senior author that it was unlikely that similar specializations in the brackish habitat were evolved by five different but evidently closely related genera, made a review necessary. Preliminary work was done by the senior author and later elaborated by the junior author as partial fulfillment of his post-graduate studies.

MATERIALS AND METHODS

The greater part of the material came from the collections of the British Museum (Natural History) and of the senior author, from whose material small series have been presented to other museums. Several institutions sent material as gifts or loans.

The photographs were taken by Mr. E. van der Vlist and other staff at the Zoölogisch Laboratorium, Rijksuniversiteit, Utrecht. Drawings of opercula were made by using a drawing-prism. In order to make camera-lucida drawings, it was necessary to separate the setae and uncini. This was achieved by putting entire animals in a few drops of 10% KOH for 12-24 hours and subsequently squashing them in glycerin-gelatin. Some figures were drawn from tufts of setae, extirpated from the animals, and preserved in glycerin-gelatin. All figures were drawn by the junior author.

Measurements, unless stated otherwise, are given in mm; meristic values are based upon counts in ten specimens minimally, unless otherwise stated (e.g., $n = 3$). References in synonymies preceded by "[?]" indicate a questionable identification in our view. The following abbreviations are used for collections: AHF, Allan Hancock Foundation, University of Southern California, Los Angeles; AM, the Australian Museum, Sydney; AMNH, the American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; MNHN, Musée Nationale d'Histoire Naturelle, Paris; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SME, Station Marine d'Endoume, Marseille; THU,

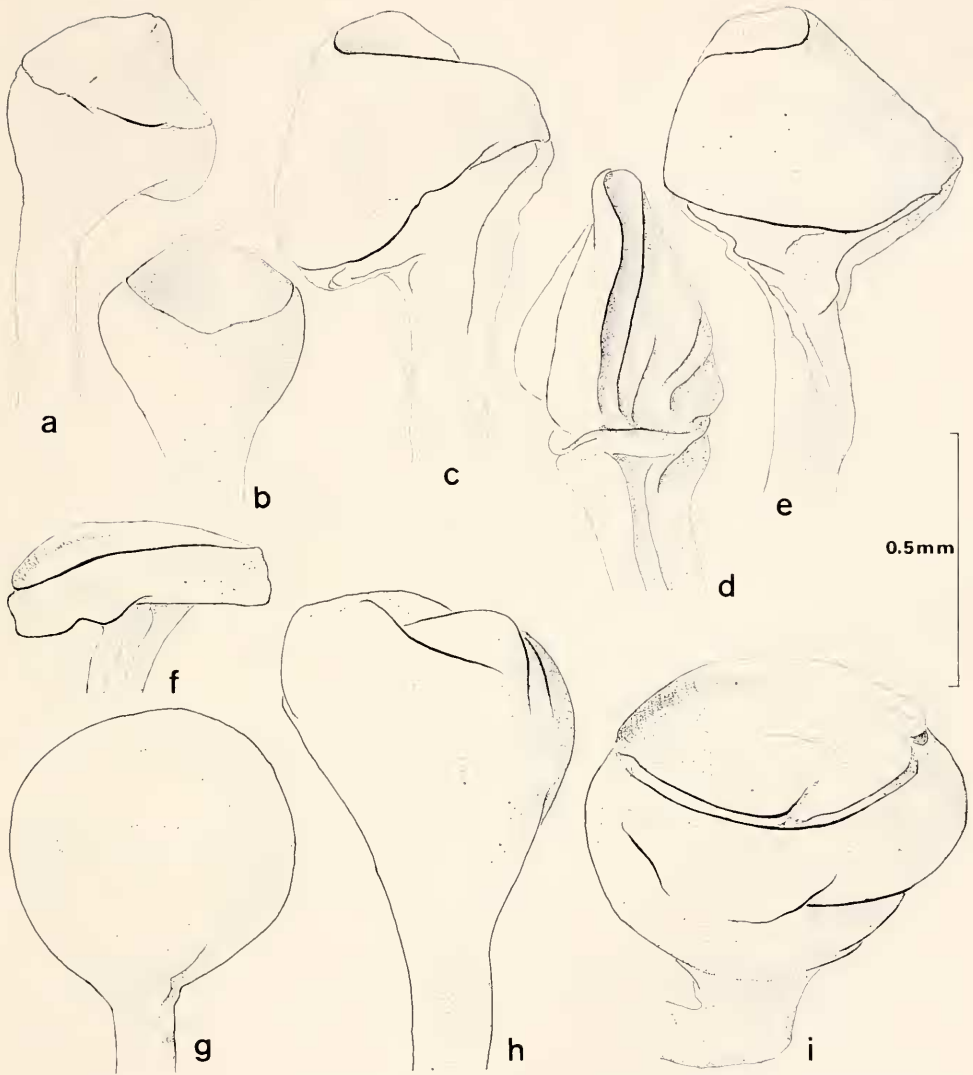


FIGURE 1. Opercula, different orientations. The specimens represented in a-e are *Ficopomatus macrodon* from Taléh-Sap; the series shows the possible development from young to old. The specimens in f-i are *F. miamiensis*: f, syntype from Miami; g, from Curacao; h-i, from Barbados, with and without horny plate. All are to the same scale.

collection of H. A. ten Hove, Utrecht; USNM, National Museum of Natural History, Smithsonian Institution Washington (formerly United States National Museum); ZMA, Instituut voor Taxonomische Zoologie, Zoologisch Museum, Amsterdam; and ZMU, Laboratorium voor Zoölogische Oecologie en Taxonomie, Zoologisch Museum, Utrecht.

TAXONOMY

Genus *Ficopomatus* Southern, 1921

Type-species: *Ficopomatus macrodon* Southern, 1921, by monotypy. Gender: masculine. Synonyms: *Mercierella* Fauvel, 1923, type-species: *M. enigmatica* Fauvel, 1923, by monotypy; *Sphacropomatus* Treadwell, 1934, type-species: *S. miamiensis* Treadwell, 1934, by monotypy; *Mercierellopsis* Rioja, 1945, type-species: *M. prietoi* Rioja, 1945, by monotypy; *Neopomatus* Pillai, 1960, type-species: *N. uschakovi* Pillai, 1960, by original designation.

Original diagnosis: "Modified setae present on the first thoracic segment, having blades provided with very stout teeth. Beneath the blades is a transverse row of more than two teeth. Uncini with relatively few teeth, the lowest of which is in the form of an elongate bifid spine. Ventral abdominal setae geniculate. Operculum fig-shaped, without any outgrowths" (Southern, 1921, p. 655).

Emended diagnosis: Tube white, gradually increasing in diameter toward anterior end and semicircular in cross-section. One or three keels sometimes present.

Thoracic segments seven, with six uncinigerous. Collar setae coarsely serrated and limbate. Remaining thoracic setae limbate. Thoracic uncini saw-like, exceptionally partly rasp-like, with six to twelve teeth visible in profile, including anterior gouged tooth. Uncinigerous tori placed in two, nearly parallel rows. Abdominal setae geniculate with denticulate edge. Abdominal uncini saw- or rasp-like, with one to four rows of teeth, six to fourteen teeth visible in profile, including anterior gouged tooth. Posterior abdominal segments without capillary setae and without dorsal glandular area.

Operculum consisting of bulbous fleshy part, terminated by horny plate; peduncle smooth, without filaments or wings, inserted just below left branchial lobe, near medial line. No pseudo-operculum present.

Collar not lobed, with entire edge, continuous with thoracic membranes which are united ventrally on anterior abdominal segments. Branchial filaments arranged in two semicircles, not united by branchial membrane. Pair of ventral mouthpalps absent.

Key to species of *Ficopomatus*

1. Operculum not "spiny" (Fig. 1) 2
- Operculum "spiny" (Fig. 2) 3
- 2(1). Operculum with conical horny cap with dorsal furrow (Fig. 1a-e); tube usually with median keel (Fig. 5e) *F. macrodon*
- Operculum without horny endplate, or with slightly concave one (Fig. 1f-i); tube without median keel (Fig. 5a, b) *F. miamiensis*
- 3(1). Operculum distally convex, "spines" curved outwards (Fig. 2a-d); thoracic membranes fused dorsally *F. uschakovi*
- Operculum distally concave, "spines" curved inwards (Fig. 2f-i); thoracic membranes not fused dorsally *F. enigmaticus*

Discussion: As already stated by Southern (1921, p. 655) the main character separating *Ficopomatus* from all other known serpulid genera is the peculiar shape of the special collar setae. A presumed difference in collar setae and presence of

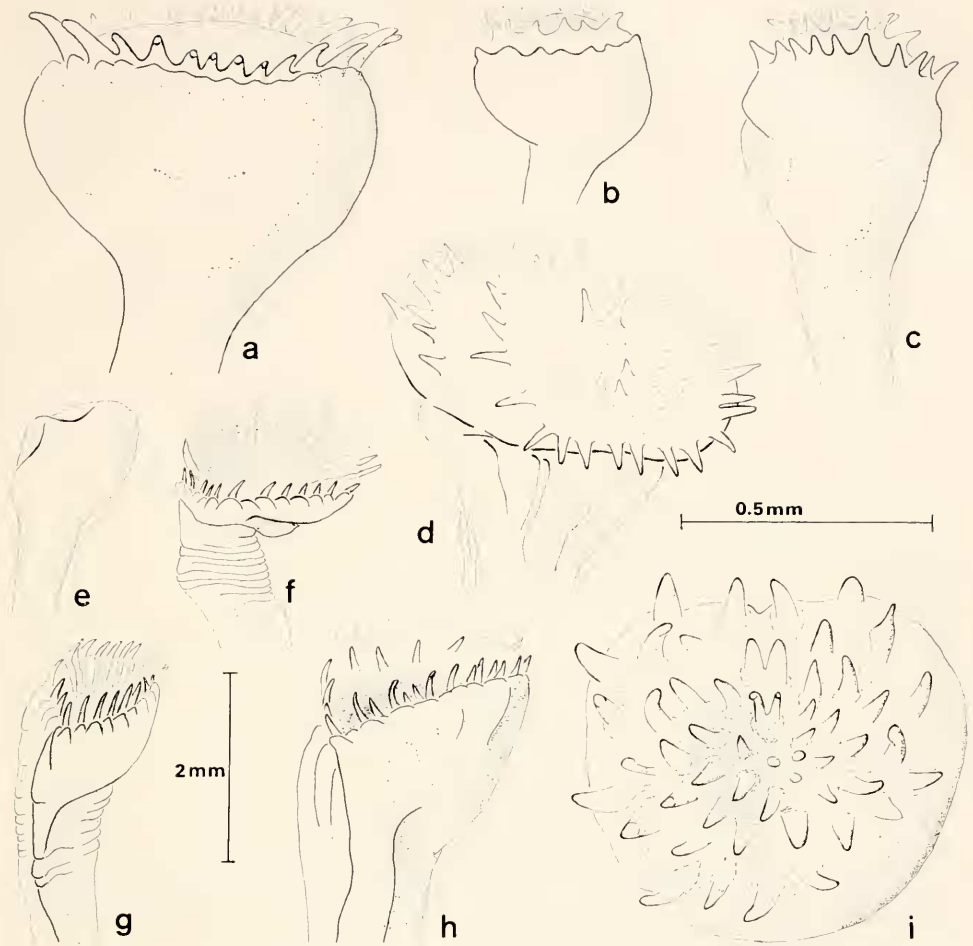


FIGURE 2. Opercula, different orientations. The specimens represented in a-d are *Ficopomatus uschakovi*: a-c, from Guadalcanal; d, paratype of var. *lingayanensis* from Luzon. The specimens in e-i are *F. enigmaticus*: e-h, from the Netherlands; i, from Uruguay. Scale in f, g, h is 2 mm; in remaining figures, the scale is 0.5 mm.

spines on the operculum were the main reasons for Fauvel's (1923, p. 429) proposing the new genus *Mercierella* for his specimens. Erroneously, Treadwell (1934, p. 340) counted only six thoracic setigers, which, along with the presumed difference in collar setae, was his main reason for erecting *Sphaeropomatus*. Rioja (1945, pp. 412-413) acknowledged the similarity of his *Mercierellopsis* with *Sphaeropomatus*, but thought it to be different in the number of thoracic setigers and in the presence of a horny endplate on the operculum of the former (not mentioned for *Sphaeropomatus* by Treadwell, although found to be present on his material). Similar reasons finally led Pillai (1960, p. 33) to describe a fifth genus, *Neopomatus*, although he recognized the similarities among four of the five genera by creating the subfamily Ficopomatinae for them (1960, p. 35). All differential diagnoses,

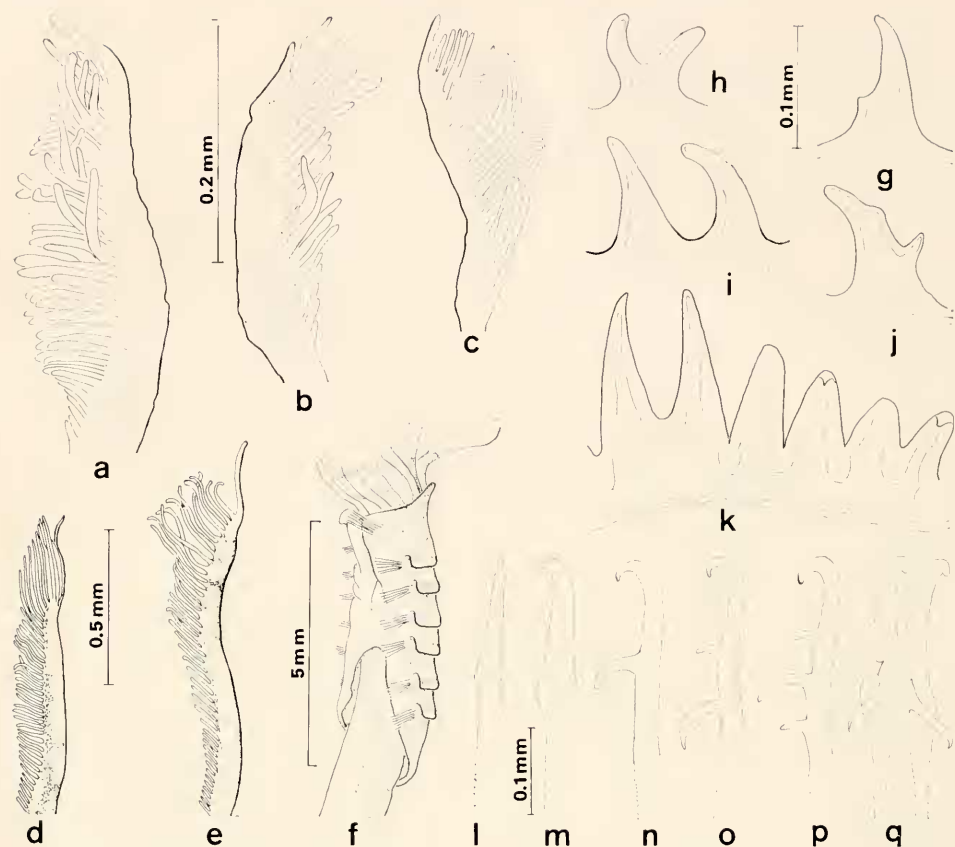


FIGURE 3. Branchial filaments (a-e); thorax (f); and variability in opercular spines (g-q). The specimens represented are: a, f-k, *Ficopomatus uschakovi* from Guadalcanal; b, *F. macrodon* from Taléh-Sap; c, *F. miamiensis* from Jamaica; and d, e, l-q, *F. enigmaticus* from the Netherlands.

given by these authors, were based upon literature only.

Straughan (1966, p. 145) held the opinion that "... there is a continuous cline between isolated populations between Sydney, where the brackish water serpulids are typical of *Mercierella*, and Brisbane, where the brackish water serpulids are typical of *Neopomatus* ...". For that reason she synonymized *Neopomatus uschakovi* with *Mercierella enigmatica*. This has been refuted by Hartmann-Schröder (1971) and Pillai (1971). Although both authors report an enormous infraspecific variability, they still maintain a generic separation of the two species. Pillai (1971) redescribed the genera, with the omission of *Mercierellopsis*.

Thus, most authors agree that there are many similarities in this group, but that there are five different genera based on differences in denticulation of collar setae, the presence of spiny or nonspiny opercula, differences in shape of collar and thoracic membranes, and presence or absence of "peristomes" on the tubes (collar-like rings which indicate the position of former peristomes).

With regard to the differences in collar setae, a considerable variation in their shape may occur within one species, even in one specimen (*e.g.*, ten Hove, 1974, Figs. 4-9, for *Hydroides norvegica* Gummerus). Extreme variability in opercula was noted by ten Hove (1970, Figs. 77, 121, 123) for *Spirobranchus polycerus* (Schmarda) and (1975, plates I-III) for *Pseudovermilia occidentalis* (McIntosh). Collar and thoracic membranes are thin, fleshy structures; their shape is dependent on the method of preservation. The presence or absence of "peristomes" may depend upon environmental conditions (Hartmann-Schröder, 1967, p. 454, for *Mercierella enigmatica*); a further example of variability of tubes, to the extent that within one species "peristomes" may be present or absent, is given by ten Hove (1973, plates I-II) for three species of *Sclerostyla* and (1975, plate VII) for *Pseudovermilia occidentalis*.

Considering that the differences between the five "genera" under discussion are certainly not greater than the above-mentioned examples of variability, and considering the striking similarities summarized in our emended generic diagnosis, it does not seem realistic to consider them as distinct. Further arguments for synonymizing these genera will be given in the various discussions following the species descriptions. In our opinion, the differences between *Ficopomatus* and other serpulid genera are too small to justify a distinction on the subfamily level. Therefore, we suggest that the subfamily Ficopomatinae Pillai (1960, p. 35) be withdrawn from recognition.

All species of the genus *Ficopomatus* may occur as solitary individuals or in dense aggregated masses. A discussion of the possible causes of mass occurrence has been given by ten Hove (1978).

Ficopomatus capensis Day (1961, pp. 552-553, Fig. 17 h-n; 1967, pp. 810-812, Fig. 38.5 j-n) definitely cannot be included in the genus, as emended above. From the figures and description it more probably should be placed in *Chitinopoma* Levinsen, emended (Zibrowius, 1969), *Chitinopomoides* Benham, or *Pseudo-chitinopoma* Zibrowius. Since these three genera are mainly characterized by the microstructure of the setae and uncini, the generic position of Day's species can only be established after a careful comparison of material of the genera concerned.

The occurrence of wide, flaring "peristomes" on the tubes of fossil serpulids was thought to be of generic diagnostic value by some palaeontologists. This has been disputed by Hartmann-Schröder (1967, p. 452). To our knowledge, "peristomes" may occur in species of the genera *Chitinopomoides* Benham, *Crucigera* Benedict, *Filograna* Oken, *Josephella* Caullery and Mesnil, *Metavermilia* Bush, *Pseudovermilia* Bush, *Serpula* Linnaeus, and *Vermiliopsis* Saint-Joseph. The tubes of *Serpula narconensis* Baird, as figured by McIntosh (1885, plate 54, Fig. 5) are very similar to those of *Ficopomatus enigmaticus*. Judging by the figures and measurements, *Mercierella? dubiosa* Schmidt (1951, p. 80, Fig. 4) might belong to *Filograna*. For similar reasons, the tube of *M. roverctoi* Schmidt (1951, p. 80, Fig. 5) is strongly reminiscent of a yet undescribed species of *Serpula* from the Caribbean. Regenhardt (1961) erected a genus, *Proliserpula*, containing species with "peristomes" and suggested a connection with *Mercierella*. In our opinion, most of his species resemble recent species of *Pseudovermilia*, as well as *Filograna*, *Serpula* and *Vermiliopsis*. *Mercierella (?) dacica* Dragastan (1966, pp. 147-150, Figs. 1-3) resembles not only *Josephella*, but also some calcareous algae.

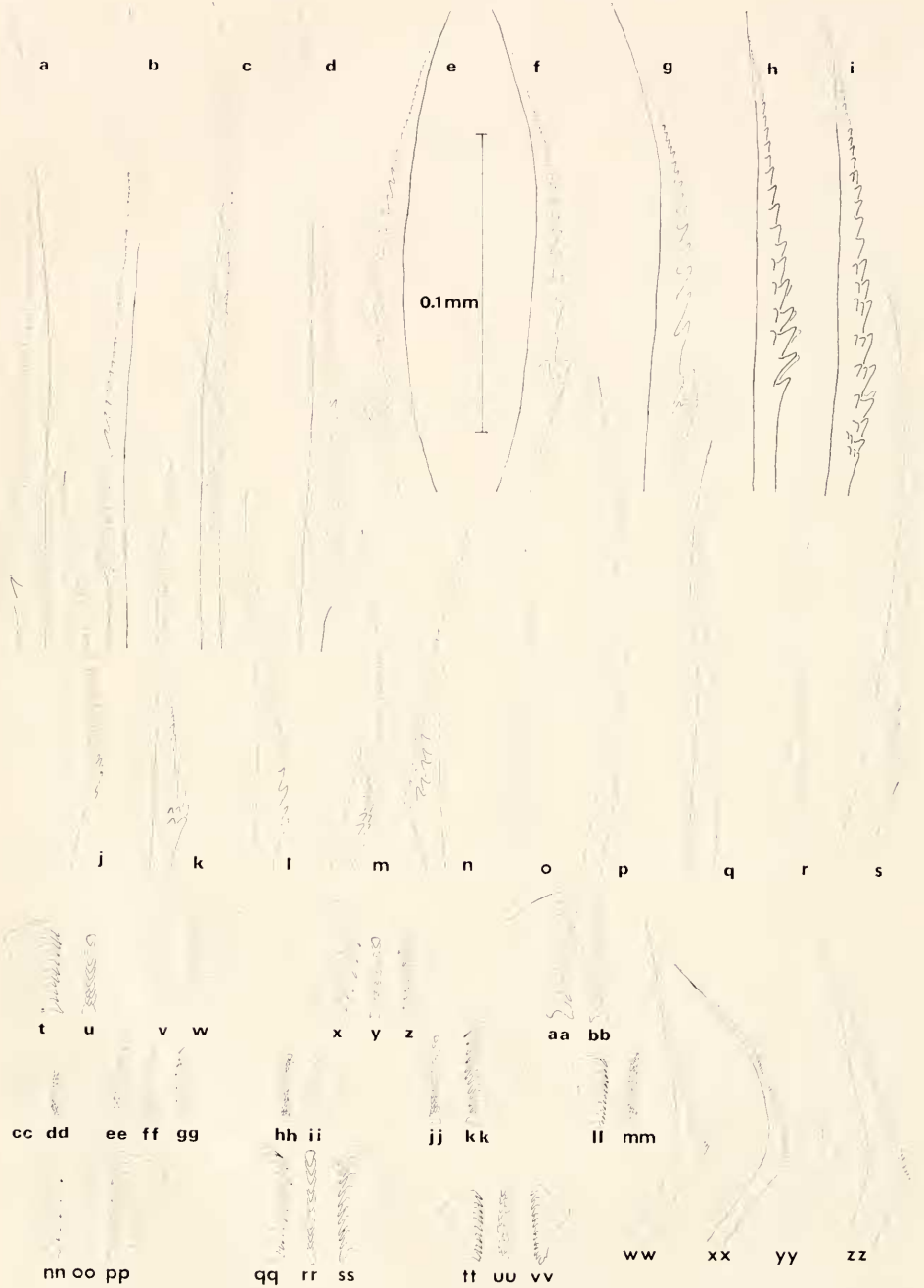


FIGURE 4. Collar setae are shown in the series, a-n, displaying all kinds of intergradations between a single row of teeth and a partial triple row; however, a prominent smooth gap be-

Ficopomatus macrodon Southern 1921

Figures 1a-e; 3b; 4e-g, o-p, t-u, cc-dd, ww; 5e

Serpulid—Annandale 1916, p. 100 [Siam, Taléh-Sap; material studied by us].

Ficopomatus macrodon Southern, 1921, pp. 655-659, plate 30, Fig. 27 A-M

[India, Cochin Backwater; extensive description]; Rioja, 1924, pp. 168-169 [no new data; comparison with *F. enigmaticus*]; McIntosh, 1926, pp. 405-423, plate 13, Fig. 3, plate 15, Fig. 3 [India, Chilka Lake; no new data; anatomical description of operculum]; Hartman, 1959, p. 575 [name only]; Pillai, 1971, pp. 115-116, Fig. 8A-F [Ceylon, Tambalagam Lake; description and comparative study].

[?] *Ficopomatus macrodon*—Fauvel, 1931, p. 1069 [India, Madras Coast, Ennur

Backwater; name only, could be *F. uschakovi*; see discussion below]; Fauvel, 1932, pp. 248-249 [India, Madras Coast, Ennur Backwater; Sunderbans; Taléh-Sap, Gulf of Siam, Stats. 11, 17, 21, 29, and 32; description; some material of Stat. 32 studied by us; see discussion below]; Fauvel, 1953, pp. 473-474, Fig. 248 c-1 [India, Madras Coast, Ennur Backwater; Cochin Backwater; Chepparan; Sunderbans; Taléh-Sap, Gulf of Siam; description; see discussion below].

Ficopomatus—Pillai, 1960, pp. 32-35 [comparative study; diagnosis].

non*Ficopomatus* sp.—Hill, 1967, pp. 303-321 [Nigeria, Lagos; name only; most likely abnormal *F. uschakovi*; see discussion below].

Mercierella enigmatica—Nelson-Smith, 1967, p. 54 (in part?) [the palaeotropical records most probably are of *F. macrodon* or *F. uschakovi*; the diagnosis and figures are of *F. enigmaticus*].

[?] *Mercierella enigmatica*—Ganapati, Lakshmana Rao, and Nagabhushanam, 1958, pp. 197-206 [India, 17°N; 83°E; name only, material is probably *F. macrodon* or *F. uschakovi*].

Material Studied. Thailand: Taléh-Sap, Annandale Collection, Stat. 32 (five isolated specimens and three small pebbles with seven specimens in tubes [BMNH 1938: 5: 7: 89-91]; ten specimens identified by P. Fauvel and H. Zibrowius [MNH]).

Tube: The tube is shining white, semicircular in cross-section. Collar-like rings of former peristomes were absent in the material studied. Most of the tubes have a high and sharp median keel (Fig. 5e); however, in a few tubes it is indistinct.

Branchiae: The branchial filaments arise from paired lobes and number about six (5-7; n = 5) on the left and seven (6-7; n = 5) on the right. They are arranged in two semicircles and are not connected by a branchial membrane. The filaments are shorter ventrally, their tips being free of pinnulae to a greater or lesser extent (Fig. 3b).

tween proximal coarse bunches of teeth and distal series of teeth is nowhere present. Posterior setae are shown as follows: o-s, other thoracic setae; t-bb, thoracic uncini; cc-vv, abdominal uncini (cc-gg, jj-kk, nn-pp, anterior segments; qq-ss, middle segments; hh-ii, ll-mm, tt-vv, posterior segments); and ww-zz, abdominal setae. Species represented are: *F. enigmaticus* from the Netherlands, a-d, s, aa-bb, nn-vv, zz; *F. macrodon* from Taléh-Sap, e-g, o-p, t-u, cc-dd, ww; *F. miamiensis* from Barbados, h-i, q, v-w, ee-ii, xx; and *F. uschakovi* from Java, j; from Guadalcanal, k-n, r, x-z, jj-mm, yy. All are to the same scale.

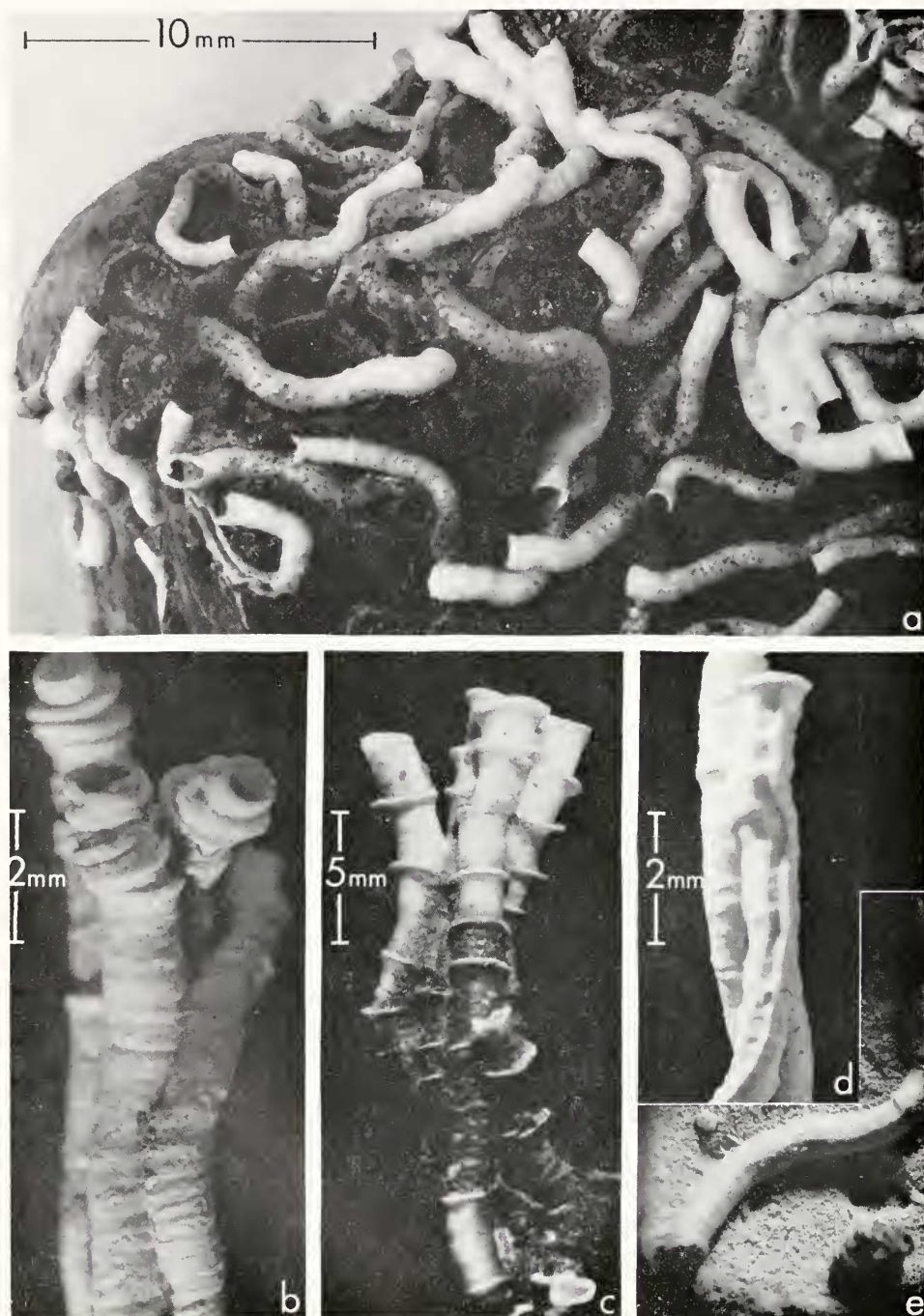


FIGURE 5. Tubes of *Ficopomatus*: a, b, *F. miamiensis* from Barbados, showing differences between two populations from Holetown river pool and from one-half mile north of Bellairs Institute; c, *F. enigmaticus* from the Netherlands; d, *F. uschakovi* from India, showing three longitudinal keels; and e, *F. macrodon* from Taléh-Sap, showing one longitudinal keel.

Peduncle: The peduncle is smooth, sometimes faintly wrinkled, especially just below the bulb of the operculum. It is subtriangular in cross-section with a shallow dorsal groove. There is a gradual transition from peduncle to opercular bulb (Fig. 1a-b).

Operculum: The operculum is a fleshy bulb, terminated by a more or less conical horny cap, which has a dorsal furrow (Fig. 1a-e). The thickness of the horny plate is positively correlated with increasing length of the cone.

Collar and thoracic membranes: The collar is rather high, not lobed, and has an entire edge. It is continuous with the thoracic membranes, which are united ventrally on the anterior abdominal segments.

Thorax: The thorax has seven segments, six of which are uncinigerous. The bundles of collar setae contain only a few setae of two types: coarsely serrated ones (Fig. 4e-g; see discussion below) and limbate ones. Subsequent fascicles of setae are larger and are in two nearly parallel rows, containing limbate setae only (Fig. 4o-p). The thoracic uncinigerous tori are arranged in two nearly parallel rows, with about 70 ($n = 2$) uncini per torus. The thoracic uncini have a single row of teeth; however, directly above the most anterior gouged tooth, there are one or two transverse rows of two or three teeth (Fig. 4t-u). There are ten to twelve ($n = 4$) teeth visible in profile. Thoracic uncini from the first row do not differ essentially from those in the last row.

Abdomen: Owing to the scanty and incomplete material, the number of abdominal segments and uncini per row could not be determined. The abdominal uncini are all rasp-like, with three to four rows of small curved teeth; about 13-15 teeth ($n = 3$) are visible in profile, including the anterior gouged one (Fig. 4cc-dd). The bundles of abdominal setae consist of two to five geniculate ones (Fig. 4ww).

Size: The length, including operculum, is at least up to 7 mm, but cannot be given more exactly owing to the incompleteness of the specimens; the width of the thorax is usually 0.5-0.7 mm ($n = 4$). The branchiae and the operculum may account for one-fifth of the entire length of the animal.

Discussion: Unfortunately the type material of *F. macrodon* was not available, and the material studied was in poor condition. Yet at least 20 collar setae have been studied.

The diagnostic value of the microstructure of the collar setae has been overstressed by several authors, which, along with some other variable characteristics, has resulted in five different genera. According to Southern (1921, p. 656, Fig. 27D-E) collar setae of *F. macrodon* have a transverse row of teeth, and a series of very coarse teeth distally, separated by a smooth gap. However, Pillai (1971, p. 116, Fig. 8D-F) indicated that the above mentioned gap occasionally may be absent. In our material this gap, if present at all, was not prominent. Thus, in all probability there is a complete cline from long smooth gap to continuous series of teeth. Consequently, this cannot be used as a distinguishing characteristic. Moreover, Hartmann-Schröder (1971, Fig. 7c-d) gives a similar variation in the collar setae of *F. uschakovi*. A considerable variation in shape and arrangement of teeth is given for *F. enigmaticus* by Rioja (1924, Fig. 16-19) and Hartmann-Schröder (1967, Fig. 4) and for *F. uschakovi* by Pillai (1960, Fig. 12C-D, I-K; 1965, Fig. 23G-I). Our studies also show a considerable variation in the microstructure of

the collar setae (Fig. 4a-n) and, after studying more than one hundred slides, each with about eight special setae, we still are incapable of distinguishing the species by their collar setae alone.

F. macrodon can be distinguished from other species in the genus by its peculiar thoracic uncini. In our opinion this feature is insufficient to justify a generic distinction (cf., *Pseudovermilia babylonia*, ten Hove, 1975, p. 96).

The operculum of *F. macrodon* resembles those of some specimens of *F. miamiensis* in having a horny endplate without spines. However, the shape of this endplate is different for both species (cf., Fig. 1).

Fauvel (1931, 1932, 1953), cited by Nelson-Smith (1967, p. 64), mentions both *F. macrodon* and *Mercierella enigmatica* from Madras. Fauvel (1932, p. 248) states, "These *Ficopomatus* tubes are rather square in section with three dorsal ridges, . . . but the animals enclosed in them are typical *Ficopomatus*". For *Mercierella enigmatica*, Fauvel (1932, p. 250) reports, "Its tube is cylindrical, . . . is neither ridged nor enlarged at the entrance." However, a re-examination of part of his material, from this locality, labelled *Mercierella enigmatica*, showed tubes with three prominent ridges, containing *F. uschakovi*. To our knowledge, tubes of *F. macrodon* generally have one longitudinal ridge only. It is evident that Fauvel's description is confusing, the more so since he figures European material (1953, p. 475, Fig. 249), and, therefore, his identifications need to be checked.

According to Annandale (1916), the type-locality Taléh-Sap is the same as the inland sea of Singgora (also spelled Sengora or Songhkla). It is located on the Malayan peninsula, on the Gulf of Siam (see Fig. 6). It appears that *F. macrodon* occurs in brackish waters adjacent to the Gulf of Bengal and the Gulf of Siam.

Ficopomatus miamiensis (Treadwell, 1934)

Figures 1f-i; 3c; 4h-i, q, v-w, ee-ii, xx; 5a-b

Sphacropomatus miamiensis Treadwell, 1934, pp. 338-341, Figs. 1-5, 9 [Florida,

Miami River; description; syntypes studied by us; see discussion below]; Hartman, 1956, p. 300 [Florida, Indian and Miami Rivers; description; material studied by us]; Hartman, 1959, p. 599 [name only]; Pillai, 1971, pp. 116-119, Figs. 8G-H, 9 A-F [studied same material as Hartman (1956); extensive description and comparative study; see discussion below]; Lacalli, 1977, pp. 300-303, Fig. 2 [embryological study; material studied by us].

Mercierellopsis prietoi—Rioja, 1945, pp. 411-417, plates 1, 2 [Mexico, Tecolutla (Gulf of Mexico); extensive description; material apparently lost; see discussion below]; Hartman, 1951, p. 120 [no new data; short diagnosis; see discussion below]; Hartman, 1954, p. 416 [name only]; Hartman, 1959, p. 582 [name only; see discussion below].

Mercierella enigmatica—Nelson-Smith, 1967, p. 54 (in part?) [Curaçao is listed in the distribution of *F. enigmaticus*; this record most probably should be referred to *F. miamiensis*; the diagnosis and figures are of *F. enigmaticus*].

Material studied. United States of America: Florida, Miami River, 17 May 1933, from carapace of freshwater shrimp, *Macrobrachium jamaicense* (Herbst), Capt. John W. Mills coll. (18 specimens, syntypes, tubes; USNM 20074, 20075, 20077; AMNH 2167; tHU 210); Florida, tributary of Indian River, Undersea Institute of

America (six specimens, many tubes; AHF; tHU 218); Florida, Vero Beach, adjacent to Indian River, artificial ponds at Entomological Research Center, 22 and 26 March 1963, 11 June 64 (40 specimens, tubes; USNM 54335-6); Florida, Miami, Coral Gables Canal, 25 March 1969, M. L. Jones coll. (one specimen; USNM 54337); Florida, northwest coast, St. Mark Wildlife Refuge, near St. Mark Lighthouse (30° 05' N; 84° 12' W), 15 Dec. 1976, 26 Feb 1977, on submerged tree limbs in brackish water ponds, salinity 11‰, P. G. Johnson coll. (28 specimens, tubes; USNM 54795; tHU 258); Louisiana, Lake Pontchartrain, mouth of industrial canal, salinity 2.5–3‰, M.A. Poirrier coll. (eight specimens, tube fragments; USNM 54794; tHU 255). Jamaica: Great Saltpond, entrance at Fort Clarence, 8 May 1973, P. Wagenaar Hummelinck coll., Stat. 1681, 0–1 m depth (50 specimens, many in tubes; BMNH 1976: 916–942; tHU 234). Barbados: Holetown River, pool near bridge, 18 Feb. 1964, P. Wagenaar Hummelinck coll., Stat. 1444 (four specimens and pebbles with tubes; RMNH 10706; tHU 235); about 1 km North of Bellairs Institute, closed lagoon, encrusting on roots and dead branches, April–May 1975, T. Lacalli coll. (six specimens, tube fragments; tHU 225). Curacao: Bottom of H.N.L.M.S. LUYMES, after one month in Caribbean waters, 9 May 1970, H. A. ten Hove coll. (15 specimens and 55 others in tubes; RMNH 10707; SME); Schottegat, east of Rijkseenheid Boulevard, opposite Zeelandia, 20 Sept. 1970, 11 Sept. 1975, H. A. ten Hove coll., Stats. 2065, 2065a, limestone boulders in sandy mud, *Caulerpa*, 10–20 cm depth (many specimens, many tubes; tHU 254). Belize [= British Honduras]: Salt Creek, approximately 8 km north of Stann Creek, 16 May 1977, M. L. Jones coll., in channel among mangroves, about 1 m depth, on living *Isognomon alatus*, temperature 32°C, salinity 31‰ (four specimens, many tubes; USNM 54980; tHU 259). Panama: Canal Zone, Pacific Third Lock, 16 April 1972, C. E. Dawson, D. L. Pawson, W. J. Byas, M. L. Jones colls., USNM Panama Survey Stat. 87–1, cobbles, rocks, on shelf adjacent to road (24 specimens: USNM 52743; tHU 233); Canal Zone, Pacific coast, Upper Miraflores Lock chamber, 26 Aug. 1974, C. E. Dawson, M. L. Jones, H. W. Kaufman, J. Rosewater colls., USNM Panama Survey Stat. 203, lock chamber walls (three specimens; USNM 54977–9).

Tube: The tube is shining white, exceptionally dull and roughened, semicircular in cross-section. There are no longitudinal ridges or keels. Normally collar-like rings, as in *F. enigmaticus*, are absent (Fig. 5a). However, in the populations from Barbados (1 km north of Bellairs Institute), Florida (Vero Beach), and Panama (Stat. 203), wide flaring "peristomes" are present (Fig. 5b).

Branchiae: The branchial filaments arise from paired lobes and number about seven (6–9) on the left and eight (6–10) on the right. They are arranged in two semicircles and are not connected by a branchial membrane. The filaments are shorter ventrally. The two rows of pinnulae become shorter toward the ends of the filaments, which are free of pinnulae to a greater or lesser extent (Fig. 3c).

Peduncle: The peduncle is smooth, sometimes faintly wrinkled, and circular or subtriangular in cross-section. There is a gradual transition between peduncle and opercular bulb (Fig. 1h).

Operculum: The operculum is spherical to fig-shaped (Fig. 1g–h), sometimes with a horny end-plate (Fig. 1f, i), which may be flat or slightly convex (see discussion below). The operculum never has spines.

Collar and thoracic membranes: The collar is high, not lobed and has an entire edge. It is continuous with the thoracic membranes, which are united ventrally on the anterior abdominal segments.

Thorax: The thorax has seven segments, six of which are uncinigerous. The bundles of collar setae contain only a few setae of two types: coarsely serrated ones (Fig. 4h-i) and limbate ones. Subsequent bundles of setae are larger and are in two nearly parallel rows, containing limbate setae only (Fig. 4q). Thoracic uncinigerous tori are arranged in two nearly parallel rows with up to 55 uncini per torus. The uncini along the entire thorax have a single row of seven (6-8) curved teeth, the most anterior one is gouged and apparently bifurcated (Fig. 4v-w).

Abdomen: The number of abdominal segments is usually about 40 (23-58, $n = 7$). The anterior two or three segments are apparently without setae or uncini. The following segments have very few uncini (five to ten). The number of uncini per row slowly increases to about 30 in the middle of the abdomen, then slowly decreases towards the pygidium (about three). The abdominal uncini of the anterior segments are partly rasp-, partly saw-like, in such a way that within a single uncinus both conditions may occur (Fig. 4ee-gg). About eight to ten teeth are visible in profile, including the anterior gouged tooth. The uncini of the posterior segments are smaller and rasp-like, with three to four rows of small curved teeth, with about 12 teeth visible in profile, including the anterior gouged one (Fig. 4hh-ii). The bundles of abdominal setae consist of three (sometimes one or two) geniculate ones (Fig. 4xx).

Size: The length, including the operculum, is about 7 mm (2.5-11). The width of the thorax is about 0.8 mm. The branchiae and the operculum usually account for one-sixth (sometimes up to one-third) of the entire length of the animal.

Discussion: As stated above, Treadwell's (1934) original description is not entirely correct; his main errors are the six thoracic setigers (in reality seven) and the entirely fleshy operculum. The opercula of 14 (out of 18) syntypes did show a horny endplate (Fig. 1f). Of about 200 specimens studied in this respect, 20% had a well-developed endplate. The endplate sometimes is difficult to see, looking more or less like a fleshy brim. Generally, however, the endplate is missing altogether.

We have the impression that there is no relation between presence or absence of endplate and the size of the specimens. Pillai's (1971, Fig. 9A-C) figures are based upon collapsed opercula without endplates (material re-examined). Although Rioja did not leave a collection (according to a personal communication from Dr. Maria Elena Caso, Instituto de Biología, Universidad Nacional de México), his figures and description of *Mercierellopsis prietoi* (1945, pp. 411-417, Figs. 1-20) are excellent, and show the conspecificity with *F. miamiensis* beyond doubt.

In contradistinction to all previous descriptions, the tube may show wide flaring "peristomes" (Fig. 5b).

Possibly Mörch's (1863, p. 353) remark on the occurrence of serpulid tubes on leaves of a freshwater plant from St. Thomas should be referred to *F. miamiensis*, although some spirorbids can occur in the brackish habitat too.

As far as is yet known, *F. miamiensis* is restricted to Atlantic tropical and sub-tropical areas in northern and middle America, and a more or less isolated locality

at the Pacific end of the Panama Canal (Fig. 6). In the brackish waters of Uruguay and Argentina, it is replaced by *F. enigmaticus*. It would be interesting to know if this is the case, too, in northern America. Since the only record of *F. enigmaticus* from the northern Gulf of Mexico is from the bottom of a boat, it is uncertain if this represents a permanent population.

Ficopomatus uschakovi (Pillai, 1960)

Figures 2a-d; 3a, f-k; 4j-n, r, x-z, jj-mm, yy; 5d

[?] Serpuliden-Röhren Ehlers, 1918, p. 250 [Aru Islands; empty tubes; see discussion below].

Mercierella enigmatica—Fauvel, 1931, p. 1069 (in part?) [India, several localities; name only; the record of Ennur Backwater is *F. uschakovi* and, perhaps, *F. macrodon*, as well; see discussion of latter species]; Fauvel, 1932, pp. 249–251 [India, Madras coast, Ennur Backwater; description; material studied by us; see discussion below]; Allen, 1953, pp. 308, 311, 315 (in part) [Australia, from Noosa, Queensland to Carnarvon, Western Australia; name only; see discussion below]; Fauvel, 1953, pp. 474–476, not Fig. 249a–o [India, Ennur Backwater; description; most likely same material as above, 1932; see discussion below]; Rullier, 1955, pp. 288–289 [Ivory Coast, Abidjan; name only; material from same locality studied by us; see discussion below]; Dew, 1959, pp. 29–31, not Fig. 8A–H (in part) [Australia, several localities; description; material from Queensland (Townsville and Noosa) is *F. uschakovi*, specimens from other localities are *F. enigmaticus*]; Straughan 1966, pp. 139–146, Figs. 2, 3b–d (in part) [Australia, several localities; Brunei; Ceylon; some of this material studied by us; Straughan's Figs. 3a and 3e are *F. enigmaticus*; see discussion below]; Rullier, 1966, pp. 95–104 (in part) [Dahomey, Cotonou; other references to *F. uschakovi* in Rullier's listing are cited by us in this synonymy]; Sandison and Hill, 1966, pp. 235–250 [Nigeria, Lagos; name only; see discussion below]; Day, 1967, p. 812 (in part?) [South Africa, Natal; diagnosis; should be checked since locality is in tropical region]; Hill, 1967, pp. 303–321 [Nigeria, Lagos; name only; see discussion below]; Nelson-Smith, 1967, p. 54 (in part?) [the paleotropical records most probably are of *F. macrodon* or *F. uschakovi*; the diagnosis and figures are of *F. enigmaticus*]; Straughan, 1967, pp. 25–40 [Australia, Queensland, Brisbane River; ecological study]; Straughan, 1968, pp. 59–64, plates 1, 2, 3A (in part) [Australia, several localities; Straughan's plate 3B is *F. enigmaticus*; see discussion below]; Gibbs, 1971, p. 203 [Solomon Islands, Guadalcanal, Lunga Point and Kominbo Bay; short diagnosis; material studied by us]; Straughan, 1971, pp. 169–175 [Australia, Queensland, North Pine River; ecological study; see discussion below]; Straughan, 1972, pp. 93–136 [Australia, Queensland, Brisbane River; ecological study; see discussion below].

[?] *Mercierella enigmatica*—Day, 1951, pp. 65–66 [South Africa, St. Lucia Estuary; name only; should be checked since locality is in tropical region]; Ganapati, *et al.*, 1958, pp. 197–206 [India, 17° N 83° E; name only; material is probably *F. macrodon* or *F. uschakovi*]; Kirkegaard, 1959, p. 105 [Nigeria, Lagos, Victoria Beach; name only; see discussion below].

non *Mercierella enigmatica*—Mesnil and Fauvel, 1939, pp. 37–38 [Kei Islands, Siboga Exped. Stat. 260, 90 m; one empty tube; see discussion below].

[?] *Ficopomatus* sp. Hill, 1967, pp. 303–321 [Nigeria, Lagos; name only; most likely abnormal *F. uschakovi*; see discussion below].

Neopomatus uschakovi Pillai, 1960, pp. 28–32, Figs. 10H, 11A–H, 12A–H, plate I, Figs. 1, 2 [Ceylon, Panadura River Estuary, Madu Ganga Estuary, Ratgama Lake; description; holotypes studied by us]; Hartman, 1965, p. 80 [name only]; Pillai, 1965, p. 172 [Indonesia, Surabaya; East Java; Madura; name only]; Pillai, 1971, pp. 118–123, 127, Figs. 9G, 10A [Ceylon, several localities; description; comparative study]; Zibrowius, 1973, p. 64 [synonymy; useful discussion].

Neopomatus uschakovi var. *lingayancensis* Pillai, 1965, pp. 170–172, Fig. 23A–I [Philippine Islands, Luzon, Lingayan Gulf and other localities; description; some paratypes studied by us].

Neopomatus uschakovi [sic]—Hartmann-Schröder, 1971, pp. 7–27, Figs. 2, 3, 5, 7b–d, 11–14 [several paleotropical localities; partial revision, synonymy].

Neopomatus similis Pillai, 1960, pp. 32–33, Fig. 12I–M, plate II, Fig. 1 [Ceylon, Negombo Lagoon; description, holotype studied by us]; Hartman, 1965, p. 80 [name only].

Neopomatus similis var. *rugosus* Pillai, 1960, pp. 33–35, plate II, Fig. 2 [Ceylon, Negombo Lagoon; description; holotype studied by us]; Hartman, 1965, p. 80 [name only].

Material studied. Sri Lanka [= Ceylon]: Panadura River Estuary, 6 Jan. 1957 (Holotype of *N. uschakovi*; BMNH 1959: 4: 14: 7); Maha Alamba, Negombo Lagoon, 18 Feb. 1959, T. G. Pillai coll. (holotype of *N. similis* var. *rugosus* and small tube on a pebble; BMNH 1959: 4: 14: 14); Ratgama Lake, 28 Feb. 1959, coconut petiole with tubes attached, T. G. Pillai coll. (ca. 25 specimens; BMNH 1959: 4: 14: 19); Cuming coll., specific locality unknown, tubes on gastropod shells (one dried operculum, empty tubes; BMNH 1965: 31: 4–5; at least 110 years in BMNH, identified by H. Zibrowius, 1972). India: Madras Coast, Ennur Backwater, Annandale coll. (four specimens in tubes, BMNH 1938: 5: 7: 92–94; also many specimens, some in tubes, MNHN; as *M. enigmatica* by P. Fauvel; as *Neopomatus* sp. by G. Hartmann-Schröder; as *N. uschakovi* by H. Zibrowius). Indonesia. Java: Specific locality unknown, 1904, P. Serre coll. (many specimens in tubes on barnacles; MNHN; as *M. enigmatica* by P. Fauvel; as *N. uschakovi* by H. Zibrowius). Philippines: Luzon, Lingayan Gulf, T. G. Pillai coll. (five paratypes of *N. uschakovi* var. *lingayancensis*; BMNH 1965: 53: 19–28). Solomon Islands. Guadalcanal: Komimbo Bay, 19 July 1965, at mouth of freshwater creek, above MTL and Lunga Point, 9 Sept. 1965, in brackish lagoon at LWM, P. E. Gibbs coll. (ca. 70 specimens, some in tubes; BMNH 1970: 830/831; as *M. enigmatica* by P. E. Gibbs, as *N. uschakovi* by H. Zibrowius). Australia. New South Wales: Yamba, 1 Sept. 1950 and Queensland: Townsville, 26 Dec. 1950, and Noosa, 1 March 1951, B. Dew coll. (10 specimens; BMNH 1955: 11: 1: 116; AM W-3777–9, 3781; as *M. enigmatica* by B. Dew; as *N. uschakovi* by H. Zibrowius and T. G. Pillai). Nigeria. Lagos: Jan. 1954 (11 specimens and many others in tubes; BMNH 1954: 3: 4: 1–50; as *M. enigmatica*; as *Neopomatus* sp., by G. Hartmann-Schröder and as *N. uschakovi* by H. Zibrowius). Ivory Coast. Abidjan: June 1955, M. Fox coll. (many specimens in tubes on pieces of

wood; BMNH 1955: 11: 1: 1-30; as *M. enigmatica*; as *Neopomatus* sp. by Hartmann-Schröder, and as *N. uschakovii* by H. Zibrowius. Netherlands. Noordwijk: on wood cast ashore on beach, 13 Oct. 1974, A. W. Lacourt coll. (many tubes and dried opercula, RMNH 07274, tHU 213).

Tube: The tube is shining white, sometimes the older parts are covered with a brownish layer of algae, presumably. It is semicircular in cross-section. At irregular intervals it bears more or less prominent collar-like rings, which indicate successive positions of the peristome. Usually there are three keels (Fig. 5d), of which the median is high and sharp, the lateral ones may be smaller; sometimes they are faint or lacking. The keels are less conspicuous toward the mouth of the tube.

Branchiae: The branchial filaments arise from paired lobes and number about eight (5-10) on the left and nine (6-11) on the right. They are arranged in two semicircles and are not connected by a branchial membrane. The filaments are shorter ventrally. The two rows of pinnulae become larger toward the end of the filaments, which is free of pinnulae to a greater or lesser extent (Fig. 3a).

Peduncle: The peduncle is smooth, sometimes faintly wrinkled, especially just below the bulb of the operculum. It is circular to subtriangular (the latter near the opercular bulb) in cross-section. There is a gradual transition from peduncle to opercular bulb, however, slightly more abruptly than in *F. enigmaticus* (cf. Fig. 2a with 2f).

Operculum: The operculum usually is spherical and radially symmetrical, sometimes with bilateral symmetry. It usually has a convex, slightly horny plate distally, which sometimes may be lacking. This end-plate is bordered by one to four (exceptionally up to eight) rows of small denticulations (Fig. 2a-d), curved outward. The denticulations ("spines") of one row may be either fused with or completely separated from each other. Sometimes the rows of "spines" are incomplete or irregular. The "spines" are randomly placed in a few specimens, and, exceptionally, cover the endplate. "Spines" with small outgrowths sometimes occur (cf. Fig. 3g, j with h, i, k).

Collar and thoracic membranes: The collar is rather high, not lobed and has an entire edge. It is continuous with the thoracic membranes, which are fused dorsally (Fig. 3f) and are united ventrally on the anterior abdominal segments. Exceptionally, there are specimens in which the thoracic membranes are not fused dorsally (one of the approximately 200 specimens studied).

Thorax: The thorax has seven segments, six of which are uncinigerous. The bundles of collar setae contain only a few setae of two types: coarsely serrated ones (Fig. 4j-n) and limbate ones. Subsequent bundles of setae are larger and are in two nearly parallel rows, containing limbate setae only (Fig. 4r). The thoracic uncinigerous tori are arranged in two nearly parallel rows, with up to 75 uncini ($n = 5$) per torus in large animals (Lunga Point). The uncini along the entire thorax have a single row of seven to nine curved teeth, the most anterior tooth gouged, apparently bifurcated (Fig. 4x-z).

Abdomen: The number of abdominal segments is usually about 40 (18-46, $n = 7$). The anterior two or three segments are apparently without setae or uncini. The following segments have very few uncini (three to four). The number of uncini per row slowly increases to about 45 in the middle of the abdomen, then

slowly decreases toward the pygidium (three to six). The abdominal uncini are rasp-like along the entire abdomen, with two rows of curved teeth anteriorly, two to three rows posteriorly; anteriorly about 10–12 teeth are visible in profile, including the anterior gouged one, posteriorly about 13 smaller ones (Fig. 4jj–mm). The bundles of abdominal setae consist of one or two to three geniculate ones (Fig. 4yy).

Size: The length, including the operculum, is quite variable. In a population from Lunga Point the length is about 10 mm (6–12 mm); the specimens from Komimbo Bay, however, are not longer than 5 mm (2–5 mm, $n = 5$). The width of the thorax is about 1 mm in the large specimens, about 0.4 mm in the small ones. The branchiae and the operculum usually account for one-quarter of the entire length of the animal.

Variations: Special attention should be given to a form differing in operculum, described by Pillai (1965) as *Ncopomatus uschakovi* var. *lingayanensis*. This usually has a bilaterally symmetrical operculum, with a cluster of one to four spines on the endplate, in the center of the ring(s) of denticulations (Fig. 2d).

Discussion: The holotype is in poor condition, apparently having been dry. The species has been confused with *F. enigmaticus*; however, Pillai (1971) and Hartmann-Schröder (1971) have already clarified this confusion and indicated that the species are geographically separated—*F. enigmaticus* occurs in subtropical/temperate areas, *F. uschakovi* in the paleotropical region. The results of our research support this opinion (Fig. 6).

In eastern Australia the northern boundary of *F. enigmaticus* and the southern one of *F. uschakovi* lies just north of Sydney, according to the material studied by Pillai (1971) and by us. In western Australia it cannot as yet be defined exactly; the population in Swan River is *F. enigmaticus*, the material mentioned by Allen (1953, p. 308) from Carnarvon might be *F. uschakovi*, since this locality lies within the tropics.

The distributions of *F. enigmaticus* and *uschakovi* indicated above suggest that it is unlikely that both species will occur together in an entirely tropical area. In juvenile specimens of *F. enigmaticus*, *miamiensis* and *uschakovi*, opercula may have no horny parts. Therefore, *Ficopomatus* sp., as cited by Hill (1967) from Nigeria, most likely is abnormal *F. uschakovi* (see Zibrowius, 1973, p. 64).

The exact boundaries between both species in Africa cannot be given, since there are considerable gaps in the known distributions.

Mesnil and Fauvel's (1939, pp. 37–38) record of an empty tube of *Mercierella enigmatica* from a depth of 90 m off the Kei Islands is very doubtful. Unfortunately, the material could not be traced, but, since many genera show tubes with "peristomes," it is more likely that this tube belonged to a different genus than that the tube was deposited two miles offshore by streams. On the other hand, the diagnosis and locality of Ehlers' (1918, p. 250) record of empty serpulid tubes from a river on the Aru Islands indicate that these tubes most likely are *F. uschakovi*.

Our record of *F. uschakovi* from the Netherlands most probably can be explained by the brisk local trade in tropical wood, and, therefore, has not been included in Figure 6.

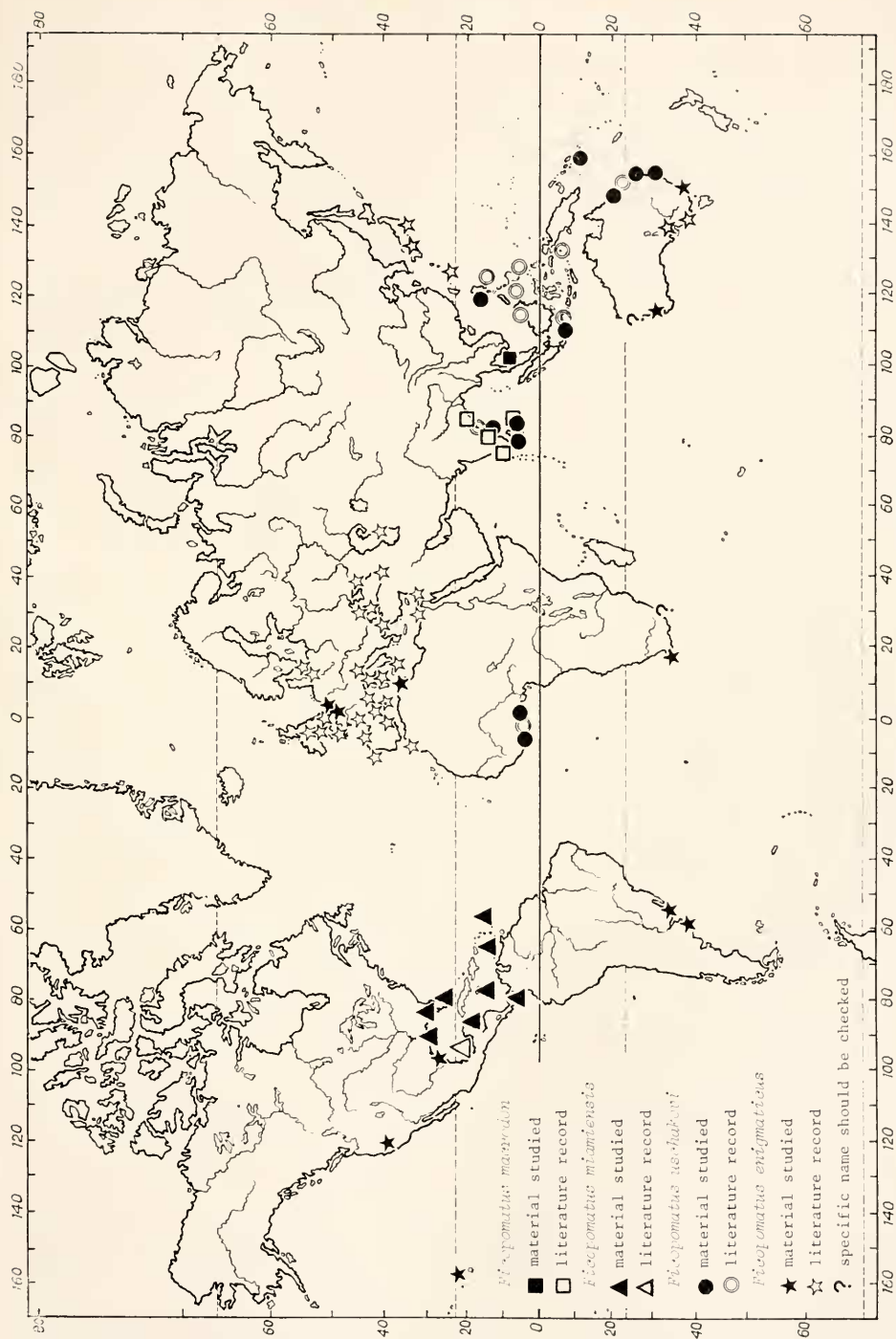


FIGURE 6. Distribution of the species of the genus *Picopomatus*.

Ficopomatus enigmaticus (Fauvel, 1923)

Figures 2c-i; 3d-e, 1-q; 4a-d, s, aa-bb, nn-vv, zz; 5c

Due to the large number of literature citations of this species, the following represents a selected synonymy and is comprised of those papers which have a special bearing on taxonomic problems and those in which material studied by us has been mentioned. It should be emphasized that *Mercierella enigmatica* from tropical regions as reported by Allen (1953), Day (1951, 1967), Dew (1959), Fauvel (1931, 1932, 1953), Ganapati, *et al.* (1958), Gibbs (1971), Hill (1967), Kirkegaard (1959), Mesnil and Fauvel (1939), Nelson-Smith (1967), Rullier (1955, 1966), Sandison and Hill (1966), Straughan (1966, 1967, 1968, 1971, 1972), at least partly, belong to one of the other three species and can be found in their respective synonymies above.

Mercierella enigmatica Fauvel, 1923, pp. 424-430, Fig. 1a-o [France, Canal de Caen; description; syntypes studied by us]; Fauvel, 1931, pp. 1068-1069 (in part) [several localities; name only; the record of India, Enmur Backwater is probably *F. uschakovi* or *F. macrodon*]; Rioja, 1931, pp. 420-424, plates 137-139 [Spain, Gandia; extensive description; account of infraspecific variability] Fauvel, 1933, pp. 185-193 [several localities; short description]; Monro, 1938a, pp. 311 and 313 [Uruguay, Arroyo de las Brujas, Canelones; name only; material studied by us]; Monro, 1938b, p. 624 [Western Australia, Pelican, Swan River; name only; part of this material studied by us]; Hartman, 1952, p. 64 [Texas, Rockport; diagnosis; material studied by us]; Allen, 1953, pp. 308, 311, and 315 (in part) [Australia, from Noosa, Queensland, to Carnarvon, Western Australia; name only; see discussion of *F. uschakovi* above]; Cognetti 1953, pp. 36-40, Fig. 1a-n [Italy, Toscana; variability of operculum]; Day, 1955, p. 448 [South Africa, several localities on the Cape; name only; part of this material studied by us]; Dew, 1959, pp. 29-31, Fig. 8A-H (in part) [Australia, several localities; the material from Queensland (Townsville and Noosa) is *F. uschakovi*; specimens from other localities are *F. enigmaticus*; description; part of this material studied by us]; Hartman, 1959, p. 582 [name only]; Pillai, 1960, p. 33 [comparison with other species]; Vuillemin, 1964, pp. 514-527, plates 1-5 [Tunisia, Lac de Tunis; extensive description of opercular variability]; Vuillemin, 1965, 554 pages, many figures [Tunisia, Lac de Tunis; thesis on their biology]; Hartman, 1966, p. 238 [Hawaii, Oahu, Honolulu, Alai Wai Canal near Waikiki; diagnosis; material from same locality studied by us]; Rullier, 1966, pp. 95-104 (in part) [list of localities to 1964, from the literature; tropical records probably are *F. uschakovi*]; Straughan, 1966, pp. 139-146, Fig. 3a, e (in part) [Australia, several localities, and California, Berkeley; specimens in Figs. 2 and 3b-d are *F. uschakovi*; see discussion above]; Day, 1967, p. 812 (in part) [South Africa, several localities on the Cape; diagnosis; the record from Natal (tropical) should be checked for it may be *F. uschakovi*]; Hartmann-Schröder, 1967, pp. 421-456, Figs. 1-24 [Europe, several localities; monograph of the species]; Nelson-Smith, 1967, p. 54, Figs. 49-50 [Southwestern United Kingdom; diagnosis; tropical localities in the distribution most probably represent other species, see discussions above]; Straughan, 1968, pp. 59-64, plate 3B (in part) [Australia, several localities; the material on plates 1, 2, and 3A are *F. uschakovi*; see discussion above]; Wolff, 1969, pp. 85-92, Figs. 1-6 [Southwest-

ern Netherlands; extensive description; part of material studied by us]; Hartmann-Schröder, 1971, pp. 7–27, Figs. 1, 4, 6, 7a, 8–10, 15–17 [Mediterranean, several localities, Black Sea, and Australia, New South Wales; partial revision and synonymy]; Orensanz and Estivariz, 1971, pp. 106–108, Figs. 47–56 [Argentina, several localities; diagnosis; part of this material studied by us]; Pillai, 1971, pp. 120–125, Fig. 10B–H [United Kingdom, Radipole Lake, Weymouth; description; comparative study of the four species]; Zibrowius, 1973, pp. 62–64 [useful discussion]; Hove, ten 1974, pp. 45–48 [Southwestern Netherlands; name only; material studied by us]; Kajihara, Hirano and Chiba, 1976, pp. 363–366 [Japan, Hamana-ko; name only]; Bailey-Brock, 1976, p. 73 [Hawaii, Oahu, several localities; name only; part of material studied by us].

Material studied. France: Canal de Caen, 19 Sept. 1922, L. Mercier coll. (three syntypes; BMNH 1928: 4: 26: 16–17). Netherlands: Vlissingen, inner harbor, L. de Wolf coll. (empty tubes; tHU 78, ZMU; as *M. enigmatica* by W. J. Wolff); Vlissingen, Keersluisburg, 6 April 1972 and 25 Sept. 1973, on piling near power station, about 1 m deep, H.A. ten Hove coll. (very many specimens, tHU 169, 191, ZMA V. Pol. 2615, SME). Tunisia: Lac de Tunis, 1969, B. Hotman coll. (many specimens; tHU 85; as *M. enigmatica* by H. Zibrowius). South Africa: Cape Town, Milnerton Estuary (two specimens, 20 tubes; BMNH 1952: 8: 10: 1; as *M. enigmatica* by J.H. Day). Australia: Western Australia, Pelican, Swan River, 17 Aug. 1935, D. L. Serventy coll. (two specimens and others in tubes; BMNH 1938: 10: 31: 29–32; as *M. enigmatica* by C. C. A. Monro and H. Zibrowius); New South Wales, Sydney, Tempe, Cooke's River, B. Dew coll. (fragmentary specimen, clusters of tubes; BMNH 1955: 9: 2: 1–20; as *M. enigmatica* by N. Tebble). United States of America: Texas, Rockport, 28 Sept. 1951, fouling on bottom of boat, G. Gunter coll. (two specimens; AHF); California, Oakland, Lake Merritt, 1931 (ten specimens, 20 tubes; tHU 232; as *M. enigmatica* by P. Fauvel); Hawaii, Oahu, Honolulu, Alai Wai Canal near Waikiki, J. H. Bailey-Brock coll. (three specimens and several others in tubes; tHU 163; as *M. enigmatica* by J. H. Bailey-Brock). Uruguay: Las Brujas, Canelones, 25 July 1937 (many specimens in tubes; BMNH 1937: 10: 15: 1–10; as *M. enigmatica* by C. C. A. Monro and H. Zibrowius). Argentina: Buenos Aires (prov.), Albufera de Mar Chiquita, desembocadura del Canal 7, 12 Oct. 1968, J. M. Orensanz coll. (32 specimens; tHU 150).

Tube: The tube is white, sometimes covered with a brown layer, presumably algae. It is semicircular to circular in cross-section. At irregular intervals it often bears wide, flaring, sometimes faint, collar-like rings indicating the successive positions of the peristome (Fig. 5c). Solitary or juvenile tubes sometimes have a faint median keel (see Cognetti, 1954, Fig. 1).

Branchiae: The branchial filaments arise from paired lobes and number about seven (5–9) on the left and eight (7–10) on the right. They are arranged in two semicircles and are not connected by a branchial membrane. The filaments are somewhat shorter ventrally. The two rows of pinnulae become larger towards the ends of the filaments, which are free of pinnulae to a greater or lesser extent (Fig. 3d–e).

Peduncle: The peduncle is smooth, sometimes faintly wrinkled, especially below the bulb of the operculum (Fig. 2g); it is subtriangular in cross-section with

a shallow dorsal groove (Fig. 2f). There is a gradual transition between peduncle and opercular bulb (Fig. 2f).

Operculum: The operculum is fig-shaped, usually bilaterally symmetrical with a distal eccentrically placed concavity. The concave part generally has a horny plate, bordered by one to four rows of spines, curved inward (Fig. 2f-h). The rows of spines may be incomplete dorsally, or somewhat irregular (Fig. 2h). The spines are randomly placed in a few specimens (Fig. 2i). Exceptionally the operculum lacks spines (Fig. 2e). The spines sometimes have one to three short radial accessory spines (Fig. 3l-q).

Collar and thoracic membranes: The collar is high, not lobed and has an entire edge. It is continuous with the thoracic membranes which are united ventrally on the anterior abdominal segments.

Thorax: The thorax has seven segments, six of which are uncinigerous. The collar setae are of two types: coarsely serrated (Fig. 4a-d) and limbate. Subsequent bundles of setae are larger and are in two nearly parallel rows, containing limbate setae only (Fig. 4s). The thoracic uncinigerous tori are arranged in two nearly parallel rows, with up to 90 uncini per torus. The uncini along the entire thorax have a single row of six to seven curved teeth; the most anterior tooth is gouged, apparently bifurcated (Fig. 4aa-bb).

Abdomen: The number of abdominal segments is usually about 60 (29-84; $n = 7$). The anterior two or three segments are apparently without setae or uncini. The following segments have relatively few uncini (21-35), the number per row increasing rapidly in the anterior one-third of the abdomen (80-120), then slowly decreasing towards the pygidium (3-20). The abdominal uncini of the anterior segments have a single row of curved teeth (six to seven), including the anterior gouged tooth; the uncini of the posterior segments are smaller, with two rows of small curved teeth, with 10-12 teeth visible in profile, including the anterior gouged one (Fig. 4nn-vv). The bundles of abdominal setae consist of two to five geniculate ones (Fig. 4zz).

Size: The length, including the operculum, is usually about 20 mm (7-44). The width of the thorax is about 1 mm (0.9-1.2). The branchiae and the operculum usually account for one-sixth of the entire length of the animal.

Discussion: *Ficopomatus enigmaticus* is mentioned in well over 150 papers, in various fields of research. We want to emphasize that some important ecological works have been based upon incorrectly identified material. Therefore, the results of this research can be evaluated only after a careful comparison with the distributional data, given in this paper (Fig. 6).

Records from Japan (Okayama Pref., Kojima Lake; Tokyo, Sumida River; Ryukyu Islands, Ishigaki-jima, Kabin Bay) have been confirmed by an excellent unpublished figure by M. Imajima.

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SUMMARY

The brackish water serpulid genera *Mercierella*, *Mercierellopsis*, *Neopomatus* and *Sphacropomatus* are synonymized with *Ficopomatus*, including four species: *F. enigmaticus*, *F. macrodon*, *F. miamiensis* and *F. uschakovi*. The geographical distributions of the species are illustrated, and the confused identity of tropical specimens has been clarified, at least in part. The generic position of *Ficopomatus capensis* is discussed. Fossil records of *Mercierella* and related genera most probably do not belong to the genus *Ficopomatus*.

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